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DESCRIPTIONS OF *TEPHRITIS FOOTEI* AND *T. HEADRICKI*, NEW SPECIES (DIPTERA: TEPHRITIDAE), WITH NOTES ON THEIR LIFE HISTORIES IN SOUTHERN CALIFORNIA

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Abstract.—***Tephritis* footei Goeden, n. sp.,** is a fruit fly (Diptera: Tephritidae) producing a single, annual generation in the flower heads of *Artemisia tridentata* Nuttall (Asteraceae) belonging to the subtribe Artemisiinae of the tribe Anthemideae in southern California. The egg, first-, second- and third-instar larvae and adults are described and figured, and selected characteristics of these stages are compared with those of other southern California *Tephritis*. Another new species of *Tephritis* belonging to the "*araneosa* complex", like *T. footei*, also is described: ***T. headricki* Goeden, n. sp.** Host plants of *T. headricki* belong to the genus *Solidago* of the subtribe Solidagininae of the tribe Astereae. The adults of these two new species are distinguished by a combination of characters involving oviscape lengths, wing patterns, wing lengths, and leg colors. The egg of *T. footei* is covered by a smooth, membraneous sheath of unknown function. The partial description of the first instar of *T. footei* is the second such for this instar in the genus *Tephritis*. Noteworthy for the first instar is confirmation of the fusion of the integumental petal with the stomal sense organ of *T. footei*, like that of *T. teerinki* Goeden. Similarly, the partial description of the second instar also is only the second for the genus *Tephritis*. The third instar has the fewest number of minute acanthae and the most integumental petals circumscribing the prothorax among four other described species. The lower, lateral, integumental petal of the cephalothorax continues around the oral cavity, like that of the third instar of *T. teerinki*. The life cycle is of the aggregative type and overwintering occurs as long-lived, sexually immature adults.

Key Words: Insecta, *Tephritis*, *Artemisia*, *Solidago*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of adults and immature stages, flower-head feeding, aggregative life cycle, seed predation, parastoids

To date, the life histories and immature stages of four species of *Tephritis* have been described in detail from southern California: *T. arizonaensis* Quisenberry (Goeden et al. 1993), *T. baccharis* (Coquillett) (Goeden and Headrick 1991), *T. joanae* Goeden (Goeden 1993, 2001b), and *T. teerinki* Goeden (Goeden 2001c). The immature stages of a fifth species, *T. stigmatica* (Coquillett), will be described in my next paper, and its biology is relatively well known (Tauber and Toschi 1965; Goeden 1988a, 1993). This paper describes the life history, adults, and immature stages of the new species, *T. footei* Goeden, along with the adults of another new species, *T. headricki* Goeden, both segregates from the "*araneosa* complex" (Foote et al. 1993).

Materials and Methods

The present study was based in part on specimens of adults belonging to the *araneosa* complex of *Tephritis* (Foote et al. 1993) reared from 1-liter samples of mature flower heads of various species of Asteraceae collected from throughout California since 1980 (Goeden 1993). The life history study and description of the immature stages of *T. footei* was based in large part on dissections of samples of mature and immature flower heads of *Artemisia tridentata* Nuttall (Asteraceae) collected north of the Hitchcock Ranch at the junction of U.S. Forest Service roads 3N16 and 3N54 in the San Bernardino National Forest (North Section) at 2,210-m elevation, southwestern San Bernardino Co., during 1995. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Two eggs, two first-, six second-, and nine third-instar larvae dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, studied and digitally photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Sixteen arenas each consisting of a clear-plastic, petri dish provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994). Each arena contained a virgin male and female obtained from emergence cages that were used for observations of courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Format used to describe the adults follows the format and method of measurement of Jenkins and Turner (1989), as used and modified by Goeden (1993, 2001c). Terminology and telegraphic format used to describe the immature stages follow Goeden (2001a, b, c), Goeden et al. (1993), Goeden and Headrick (1991), Goeden and Teerink (1999), Teerink and Goeden (1999), and our earlier works cited therein. The holotypes and allotypes together with 74 and 25 reared paratypes of *T. footei* and *T. headricki*, respectively, have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The holotypes, allotypes, and 22 and 35 paratypes were used for measurements to describe *T. footei* and *T. headricki*, respectively. All remaining paratypes and voucher specimens not designated as paratypes, voucher specimens of immature stages, and reared parasitoids of *T. footei* reside in my research collections. Means ± SE are used throughout this paper. Digitized photographs used to construct text figures were processed with Adobe Photoshop® Version 5.

Results and Discussion

Taxonomy

The following key couplets modifying couplet 6 and replacing couplet 17 in the

key of Foote et al. (1993), and replacing couplets 10 and 17 as previously modified by Goeden (1993, 2001c), enables one to distinguish these two new species. The three-digit, figure numbers in couplets 6, 10a, 18, and 19 refer to Foote et al. (1993), not to the present publication. The strike-throughs indicate parts of the original key that I suggest deleting.

6. Preapical brown area of wing interrupted by numerous round subhyaline spots (fig. 428, c); ~~dark pattern in cell r1 immediately posterior to pterostigma usually with at least 1 yellowish or hyaline spot (fig. 429, b); if no such spot present~~ anterior arm of Y-shaped mark at wing apex may be broken or conspicuously narrower than posterior arm (fig. 429, d) . . . 7
– Preapical brown area of wing usually with at most a few round subhyaline spots, its appearance never obscured by them (fig. 430, b); ~~dark pattern in cell r_1 immediately posterior to pterostigma unmarked (fig. 430, a);~~ Y-shaped mark in wing apex rarely broken as above 10
10. Anal lobe with dark markings of wing usually extending to wing margin 10a
– Anal lobe with dark markings of wing usually not, or only very faintly and narrowly, extending to wing margin 11
10a. Wing with hyaline spot in basal end of cell r_{4+5} large, oval to quadrate, and extended from vein R_{4+5} to vein M (often broadly based on the latter), usually contiguous with the hyaline area in cell r_{2+3} directly anterior to it; at least some of hyaline spots along margin of anal lobe wider than half the width of anal lobe; wing pattern as in Goeden (1993) . . . . . *joanae* Goeden
– Wing with hyaline spot in basal end of cell cell r_{4+5} anterior to vein dm-cu, smaller, round or oval, and not extended from vein R_{4+5}, but sometimes touching vein M (fig. 430, c); hyaline spots along margin of anal lobe usually less than half the width of this lobe . . . . . *signatipennis* Foote
17. Wing length of females usually under 2.6 mm; of males, usually under 2.3 mm (Fig. 1A) . . . . . *footei* Goeden, n. sp.
– Wing length of females usually exceeding 2.6 mm; of males, usually exceeding 2.3 mm 18
18. Wing with hyaline spot in basal end of cell r_{4+5} large, oval to quadrate, and extending from vein R_{4+5} to vein M (often broadly based on the latter), usually contiguous with the hyaline area in cell r_{2+3} directly anterior to it (fig. 437) . . . . . *arameosa* (Coquillett)
– Wing with circular, elliptical, ovate, or bell-shaped spot in cell r_{4+5} extending anteriorly from vein M, but usually not touching vein R_{4+5} 19
19. Femora, especially those of hind legs, dark tomentose; ~~frons reddish brown tomentose;~~ wing pattern as in fig. 438 . . *ovatipennis* Foote
– Femora all or mostly yellow~~; frons mostly white to yellow tomentose~~ 20
20. Oviscape two to three times as long as terminal abdominal tergite; hyaline spot in cell r_{4+5} anterior to vein dm-cu elliptical, oval, or bell-shaped and usually extending anteriorly from vein M more than two-thirds across cell r_{4+5}; wing pattern as in Goeden (2001c) . . . . . *teerinki* Goeden
– Oviscape only slightly longer than the terminal abdominal tergite; hyaline spot in cell r_{4+5} anterior to vein dm-cu, smaller, round or oval, and may not touch vein M (Fig. 1B) . . . . . *headricki* Goeden, n. sp.

Tephritis footei Goeden, new species
(Figs. 1A, 2–6)

Adult female.—*Head:* In profile, 1.1 to 1.3 times as high as long, face distinctly protruding below antennae, face and frons meeting at an angle of ca. 120°, gena below eye 0.18 to 0.24 times eye height, genal bristle and most genal setulae light brown; occiput slightly swollen; frons white to light yellow pollinose, white to greyish pollinose mid-dorsally and laterally, about 0.4 mm wide at vertex, narrowing to 0.3 mm at antennal bases, and 0.2 to 0.3 mm long; the two frontal setae dark brown to black; posterior orbital seta white, 0.4 to 0.7 times as long as anterior orbital seta; inner vertical seta dark brown, 0.5 to 0.7 times as long as head height, outer vertical bristle white, 0.2 to 0.3 times as long as head height; face, including antennal foveae, white; palpi and labellum light yellow to dark ocherous, sometimes tinged reddish, with four to seven, prominent, dark brown to black setulae apically; antenna 0.6 to 0.8 times as long as face at midline, yellow to dark ocherous, sometimes reddish, arista dark brown except base ocherous.

Thorax: Scutum, scutellum, and pleural

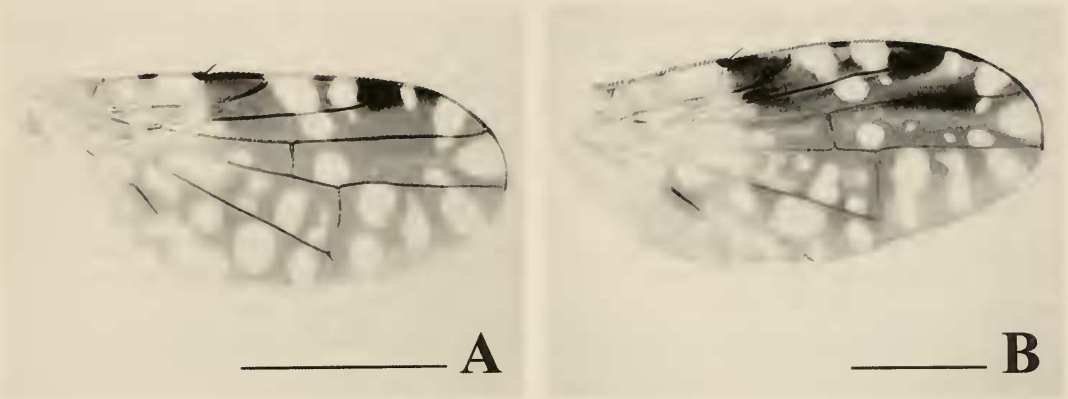

Fig. 1. (A) Right wing of *Tephritis footei* female; (B) Right wing of *T. headricki* female. Lines = 1 mm.

sclerites gray pollinose over shiny black ground-color, sometimes with single, slightly darker, faint, narrow, medial dorsolongitudinal stripe and faint lateral stripe through anterior dorsal central bristle; short, white setulae invest entire scutum; complement of thoracic bristles usual for the genus, all dark brown or black except posterior notopleural bristle, white; subscutellum and mediotergite black pollinose; scutellar setulae shorter and inserted closer to each other than are scutal setulae; scutellum bare centrally, setulae present only laterally; halteres yellow. Legs, especially femora, dark tomentose; hind tibia dark with parallel rows of black setulae; hind femur with black setulae on posterior sixth. Wing length 2.0–2.2 mm, wing pattern as in Fig. 1A, with a prominent hyaline area immediately distad of pterostigma extended from costal margin posterior to and touching vein R_{4+5}, but never extending to vein M; instead, usually round to oval, hyaline spot in basal end of cell r_{4+5} arising on and nearly always touching vein M, and usually extending at least halfway across cell r_{4+5}; dark area in pterostigma extending posteriorly to vein M and covering crossvein r-m, very rarely with hyaline markings; crossvein r-m removed from crossvein dm-cu by about its own length; large hyaline markings occupy most of cell m and extend posteriorly to posterior wing margin, as do large hyaline markings in cell cua_1, which do not cross vein CuA_1, but anteriorly divide into hyaline spots in cell dm; anal lobe mostly hyaline.

Abdomen: All tergites gray pollinose except T_6, which sometimes has shiny, black spot posteromedially, but otherwise is concolorous with mediotergite, other tergites without pattern; densely covered with colorless setulae inserted much closer to each other than their average length, becoming longer laterally and posteriorly; two or three long, hyaline to light or dark brown setae laterally along posterior margin of last abdominal tergite; oviscape flat, dark brown or black, with setulae on basal ⅔ similar to those on abdominal tergites, apical third with extremely fine, short black setae; oviscape in dorsal view 1.1 to 1.9 times as long as last abdominal tergite and 1.2 to 1.7 times as wide at base as long.

Male.—Similar to ♀ in all respects except wing length 1.7–2.1 mm; genitalia ocherous brown to black, subshining.

Variation.—Examination of reared *T. footei* with intact setation confirmed that the holotype, allotype, and most adults had two pairs of black frontal setae; however, one (1%) of 80 ♀ paratypes had five frontal setae, i.e., two pairs plus a third, weak, black seta inserted ventral to the other two pairs. One (1%) of 85 ♂ paratypes had three frontal setae, and another ♂ paratype had two pairs of frontal setae, one of which in the ventral pair was weak and white.

The right wings of the 80 ♀ paratypes varied from 1.7 to 2.6 mm in length, but 77 (96%) ♀ paratypes measured ≥ 1.8 and ≤ 2.4 mm; whereas, the right wings of the 85 ♂ paratypes varied from 1.7 to 2.3 mm in length.

Only one (1%) of the 80 ♀ paratypes had a single, faint, hyaline spot in cell r_1 within the dark area extending posteriorly from the stigma in one wing. Likewise, one (1%) of the 85 ♂ paratypes had one, faint, hyaline spot in cell r_{2+3} within this dark area in one wing.

The antennae of three (3.8%) of the 80 ♀ paratypes were tinged reddish, as were the first flagellomeres only of another 14 (17.5%) of the ♀ paratypes and the scape and peduncle of another ♀ paratype (1%). The labellum and palpi of four of these same 18 ♀ paratypes also were tinged reddish, as was the labellum alone of two more of these 18♀ paratypes, and the palpi of another one of the 18 ♀ paratypes. The antennae of four (4.9%) of the 85 ♂ paratypes were tinged reddish, as were the first flagellomeres only of one (1%) of the 85 ♂ paratypes and both the scape and peduncle of another (1%) ♂ paratype. The labellum and palpi of three of these same six ♂ paratypes also were tinged reddish, as was the labellum alone of the other three of these same six ♂ paratypes.

An additional four ♂ of the 85 ♂ paratypes examined bore the thalli of a benign, ectoparasitic fungus, *Stigmatomyces* sp. (Ascomycetes: Laboulbeniaceae), a genus reported from California by Goeden and Benjamin (1985).

Diagnosis.—The main morphological characters distinguishing the adults of *T. footei* from all other North American species north Mexico are its short wing length and the dark band in the wing extending obliquely from the pterostigma to cover vein r-m (Fig. 1A), which usually is free of hyaline spots. The wing length of *T. footei* is at least 1 mm shorter than that of *T. headricki* Goeden n. sp. described below, and the femora of *T. footei* are dark, not yellow like *T. headricki.* An elliptical, ovate, or bell-shaped, hyaline spot in cell r_{4+5} extending anteriorly from vein M, but not touching vein R_{4+5} (Fig. 1A), instead of a large oval to quadrate, hyaline spot in basal end of cell r_{4+5} extending from vein R_{4+5} to vein M (often broadly based on the latter), and usually contiguous with the hyaline area in cell r_{2+3} directly anterior to it, further distinguishes *T. footei* from the smallest specimens of *T. araneosa* (Coquillett).

The host relations of *T. footei, T. headricki,* and *T. araneosa* apparently also differ, as discussed in the next section. Indeed, as Foote et al. (1993) stated (p. 196), "... *araneosa* belongs to a complex of closely related species, the precise identification of which may never be attained without extensive biological studies." Foote (1960) described three of these, i.e., *candidipennis* Foote, *ovatipennis* Foote, *signatipennis* Foote, to distinguish those larger species with longer oviscapes, and Blanc (Foote and Blanc 1979) described another, *leavittensis* Blanc, on the basis of additional characters. Goeden (1993, 2001c) described *T. joanae* and *T. teerinki,* (respectively) two more of those *Tephritis* species with longer oviscapes. I also describe below in addition to *T. footei,* another new species with a shorter oviscape belonging to the "*araneosa* complex," i.e., *T. headricki.* Unfortunately, I have not been able to study its life history and immature stages, but am able to distinguish it morphologically, as noted above, as adults reared from a separate, different tribe of host plants in California.

Types.—Holotype: ♀; N(orth) of Hitchcock Ranch at 2,207-m (7,240-feet) (elevation), S(an) Bernardino Nat(ional) F(o)r(e)st, S(an) Bernardino Co(unty); T(ownship) 3N(orth), R(ange)1W(est), S(ection) 25; 27.x.1993; R. D. Goeden, coll. (hereafter RDG, coll.)/J. A. Teerink, coll. (hereafter JAT, coll.); reared from flower head of *Artemisia tridentata.* Allotype; ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 8 ♂ and 6♀; same data as holotype (5 ♂ and 5 ♀ to USNM). 1 ♀; same data as

holotype, except 31.viii.1995; RDG/JAT, coll. (1 ♀ to USNM). 1 ♂ and 6 ♀; same data as holotype, except 13.ix.1995; RDG/JAT, coll. (3 ♀ to USNM). 3 ♂ and 2 ♀; same data as holotype, except 12.x.1995; RDG/JAT, coll. (1 ♂ and 1 ♀ to USNM). Unless otherwise indicated the following specimens also were reared from flower head of *A. tridentata*. 16 ♂ and 14 ♀; Onyx Summit at 8,370 ft (2,551 m), S. Bernardino Nat. Forest, S. Bernardino Co.; T1N, R3E, S12; 27.x.1993; RDG/JAT, coll. (6 ♂ and 6 ♀ to USNM). 6 ♂ and 4 ♀; St. Hwy. 38 N(orth)W(est) of Onyx Peak at 2,323 m (7,620 feet); S. Bernardino Nat. Frst., S. Bernardino Co.; T2N, R2E, S35; 27.x.1993; RDG/JAT, coll. (3 ♂ and 2 ♀ to USNM). 6 ♂ and 8 ♀; along road to Big Pine Flat (U. S. F(orest) S(ervice) Road 3N14) at 1,747 m (5,730 feet), S. Bernardino Nat. Forest, S. Bernardino Co.; T2N, R2W, S1; 27.x.1993; RDG/JAT, coll. (3 ♂ and 4 ♀ to USNM). 2 ♀; along road to Big Pine Flat (USFS Road 3N16) at 1,902 m (6,240 feet), S. Bernardino Nat. Forest., S. Bernardino Co., T2N, R1W, S6; 27.x.1993; RDG/JAT, coll. (1 ♀ to USNM). 17 ♂ and 12 ♀; E(ast) of Big Pine Flat Station (along) USFS Road 3N16 at 2,039 m (6,690 feet); S. Bernardino Nat. Forest., S. Bernardino Co., T5N, R1W, S29; 27.x.1933; RDG/JAT, coll. (7 ♂ and 4 ♀ to USNM). 4 ♂; same data as preceding entry, only all infected with *Stigmatomyces*; 9.viii.1995; (2 ♂ to USNM). 11 ♂ and 12 ♀; E(ast) of Big Pine Flat Station at 2,149 m (7,050 feet); S. Bernardino Nat. Forest, S. Bernardino Co., T5N, R1W, S28; 27.x.1993; RDG/JAT, coll. (6 ♂ and 6 ♀ to USNM). 6 ♂ and 5 ♀; Arrastre Flat at 2,225 m (7,300 feet); S. Bernardino Nat. Forest, S. Bernardino Co., T3N, R1E, S34; 27.x.1993; RDG/JAT, coll. (3 ♂ and 2 ♀ to USNM). 6 ♂ and 6 ♀; Junction (State) H(igh)w(a)y 38 and Heartbar R(oa)d (U. S. F(orest) S(ervice) Road 1N02) at 2,051 m (6,730 feet), S. Bernardino Nat. Forest, S. Bernardino Co.; T5N, R1W, S29; 27.x.1993; RDG/JAT, coll. (3 ♂ and 3 ♀ to USNM). 2 ♂ and 1 ♀; SE of Holcomb Valley Campground at 2,170 m (7,190 feet); S. Bernardino Nat. Forest, S. Bernardino Co., T2N, R1E, S4; 27.x.1933; RDG/JAT, coll. (1 ♂ to USNM). 1 ♂; Cooncreek Jumpoff at 2,192 m (7,190 feet); S. Bernardino Nat. Forest, S. Bernardino Co.; T1N, R2E, S22; 27.x.1993; RDG/JAT, coll. (1 ♂ to USNM).

Etymology.—This tephritid is named for an early mentor, Richard H. Foote, who encouraged my study of the nonfrugivorous Tephritidae of California, and whose many taxonomic writings provided examples of careful craftsmanship and a firm foundation and guidance for my own studies, especially those on *Tephritis* and *Trupanea* spp.

Tephritis headricki Goeden, new species
(Fig. 1B)

Adult female.—*Head:* In profile, 1.1 to 1.4 times as high as long, face distinctly protruding below antennae, face and frons meeting at an angle of ca. 120°, gena below eye 0.13 to 0.18 times eye height, genal bristle and most genal setulae light brown, some hyaline; occiput slightly swollen; frons white to ocherous pollinose, contrasting white to dark ocherous mid-dorsally and laterally, 0.5–0.6 mm wide at vertex, narrowing to about 0.4 mm at antennal bases, and 0.3 to 0.4 mm long; the two frontal setae dark brown to black; posterior orbital seta white, 0.6 to 0.8 times as long as brown anterior orbital seta; inner vertical seta brown, about 0.7 times as long as head height, outer vertical bristle white, 0.2 to 0.3 times as long as head height; face, including antennal foveae, white to reddish; palpus and labellum light yellow to dark ocherous, sometimes tinged reddish, with four to seven, prominent, brown setulae apically; antenna about 0.7 as long as face at midline, yellow to dark ocherous, sometimes reddish, arista brown except base ocherous.

Thorax: Scutum and pleural sclerites light-gray pollinose anteriorly, scutum darkening to golden brown pollinose posteriorly, all over shiny, dark brown to black ground-color; short, white setulae invest en-

tire scutum; complement of thoracic bristles usual for the genus, all light to dark brown except posterior notopleural, white; scutellum golden brown medially, dark anteriorly along juncture with scutellum and dark apically, ocherous posteriolaterally, ventral half of subscutellum light-gray pollinose, dorsal half pale ocherous, mediotergite shiny black laterally and ventrally, dorsocentrally light-gray pollinose; scutellar setulae similar in length, but inserted closer to each other than scutal setulae; scutellum bare centrally, setulae present only laterally; halteres yellow, ocherous basally. Legs, yellow; hind tibia with parallel rows of brown setulae; hind femur with brown setulae on posterior fifth. Wing length 3.4 to 3.7 mm, wing pattern as in Fig. 1B, with a prominent hyaline area immediately distad of pterostigma extending from costal margin posterior to and touching vein R_{4+5}, with round to oval, hyaline spot in basal end of cell r_{4+5} just touching or slightly separated from vein M and usually only half or two-thirds as wide as cell r_{2+3} (Fig. 1B); dark area in pterostigma extending posteriorly to vein M and covering crossvein r-m, usually with no or one or two, faint to small, but discrete, hyaline spots in cell br; crossvein r-m removed from crossvein dm-cu by about its own length; large hyaline markings occupy most of cell m and extend posteriorly to posterior wing margin, as do large hyaline markings in cell cua_1, which may cross vein CuA_1, or occupy as separate hyaline spots, most of cell dm; anal lobe usually hyaline along wing margin or occasionally very faintly patterned with large, hyaline spots.

Abdomen: All tergites light-gray pollinose, concolorous with dorsocentral part of mediotergite, without pattern; densely covered with colorless setulae inserted much closer to each other than their average length, becoming longer laterally and posteriorly; two or three, long, hyaline to light or dark brown setae along posterior margin of last abdominal tergite; oviscape flat, dark-brown to black, with setulae on basal ⅔ similar to those on abdominal tergites, apical third with extremely fine, short dark brown setae; oviscape in dorsal view 1.2 to 1.8 times as long as last abdominal tergite and 1.2 to 1.9 as wide at base as long.

Male.—Similar to ♀ in most respects except wing length 3.0–3.6 mm; genitalia ocherous to dark brown, subshining.

Variation.—Examination of reared *T. headricki* with intact setation confirmed that the holotype, allotype, and all paratypes except one ♀ had two pairs of black frontal setae; this female had a third pair of short, white setae between the other two pairs of frontal setae.

Eight (50%) of the 16 ♀ types had no hyaline spot, however faint, in cells r_1, r_{2+3}, or br within the dark area extending posteriorly from the stigma in both wings. Two (13%) of the 16 ♀ types had one faint hyaline spot in cell r_{2+3} within this dark area in only one wing. Eight (50%) of the 16 ♀ types had one or two, faint to small, but discrete, hyaline spots in the apex of cell br, basad of crossvein r-m. In comparison, eight (35%) of 22 ♂ types had no hyaline spot, however faint, in cells r_1, r_{2+3}, or br within the dark area extending posteriorly from the stigma. Only one (5%) of the 22 ♂ types had one, small, discrete and two, faint hyaline spots in cell r_{2+3} within each dark area, respectively, in its wings. And, 15 (68%) of the 22 ♂ types had one or two, faint to prominent, hyaline spots in the dark area at the apex of cell br, basad of crossvein r-m.

The hyaline spot in the basal end of cell r_{4+5} reaches vein M posteriorly in seven (44%) of 16 ♀ types, but was slightly separated from vein M in the remaining nine (56%) 16 ♀ types. Likewise, the hyaline spot in the basal end of cell r_{4+5} reaches vein M posteriorly in 13 (59%) of 22 ♂ types, but was slightly separated from vein M in another eight (36%) of 22 ♂ types. The one remaining ♂ type had one wing in each category.

The anal lobe of only one (6%) of the 16 ♀ types contained a very faint pattern with

large hyaline spots that extended to and along the wing margin; whereas, three (14%) of the 22 ♂ types showed this condition.

The first flagellomeres of the antennae of nine (56%) of 16 ♀ types were tinged reddish, as were both pedicels of still another (6%) of the ♀ types. The labellum and palpus of three of these same 10 ♀ types also were tinged reddish, as was the labellum or palpi alone of two other, separate ♀ paratypes. The antennae of four (18%) of the 22 ♂ types were tinged reddish, as were the first flagellomeres only or pedicels only of another two each (9 and 9%) of the 22 ♂ types. The labellum and palpus of 10 (45%) of these 22 ♂ types also were tinged reddish, as was the labellum alone or palpi alone of one each (5 and 5%) of these 22 ♂ types. As some, but not all specimens of *T. araneosa* and *T. ovatipennis* (unpublished data) as well as *T. footei* and *T. headricki* had reddish colored head parts, this character is removed from couplet 19a describing *T. ovatipennis* in my revision above of the key to *Tephritis* in Foote et al. (1993). This reddish coloration apparently lies on a continuum of colorations from white to yellow to ocherous to reddish to brown to black seen in *Tephritis*.

Diagnosis.—The main morphological characters distinguishing the adults of *T. headricki* from all other North American species of *Tephritis* north Mexico are a combination of a round or ovate, hyaline spot in cell r_{4+5} anteriorad of vein M, and not touching vein R_{4+5} (Fig. 1B); the dark band from pterostigma to vein M extending obliquely to cover vein r-m (Fig. 1B); yellow femora; and an oviscape only about twice as long as the last abdominal tergite. The femora of *T. ovatipennis*, especially those of the hind legs are dark grey to black tomentose, not yellow (Foote et al. 1993). Moreover, *T. ovatipennis* and *T. teerinki* belong to those larger congeners in the "*araneosa* complex" (Foote 1960, Foote et al. 1993) with long oviscapes, not like those of *T. araneosa* with an oviscape "... only slightly longer or shorter than, or equal to, the terminal abdominal tergite . . .". In this last regard, of 62 *T. araneosa* reared from four species of *Artemisia* other than *A. tridentata* (see discussion of hosts below), none had oviscapes shorter than the terminal abdominal tergite, only one (5%) was equal, and the remainder had oviscapes from 1.1 to 1.7 times as long as the terminal abdominal tergite. Another grouping of 104 *T. araneosa* reared from three *Chrysothamnus* spp. and one *Ericameria* spp. (which I could not distinguish morphologically as another new species; see discussion of hosts below) also contained none with an oviscape shorter than or equal to the terminal abdominal tergite. The oviscapes of these 104 females varied from 1.1 to 2.3 times as long as the terminal abdominal tergites. No obvious distinctions in measurements or perceived characters of these two groups could be correlated with their distinctive host-plant taxonomic affinities. These two groups represent what remains of *T. araneosa* after the removal of segregates with longer oviscapes by Foote (1960), Foote and Blanc 1979), and Goeden (1993, 2001c), and two more species with shorter oviscapes in the present paper. This "residual" *T. araneosa* probably contains at least one more undescribed species.

Types.—Holotype: ♀; Dead Man Creek at 2,500 m (elevation), Inyo National Forest, Mono County; T(ownship)3S(outh), R(ange)27E(ast), S(ection)5; 9.x.1986; R. D. Goeden, coll. (hereafter RDG, coll.); reared from flower head of *Solidago canadensis* L. Allotype: ♂, same data as holotype (USNM). Paratypes: CALIFORNIA: 8 ♂ and 8♀; same data as holotype (5 ♂ and 5 ♀ to USNM). 7 ♂ and 5 ♀; Beasore Meadow off Beasore Road 25 km N(orth)E(ast) of Bass L(ake) at 1,960 m, Sierra National Forest, Madera County; T6S, R23E, S5; 16.ix.1988; RDG, coll.; reared from flower heads of *S. canadensis* (4 ♂ and 3 ♀ to USNM). 2 ♀; along Upper Deadman Creek at 2,496 m; Inyo National Forest, Mono County; T3S, R27E, S6;

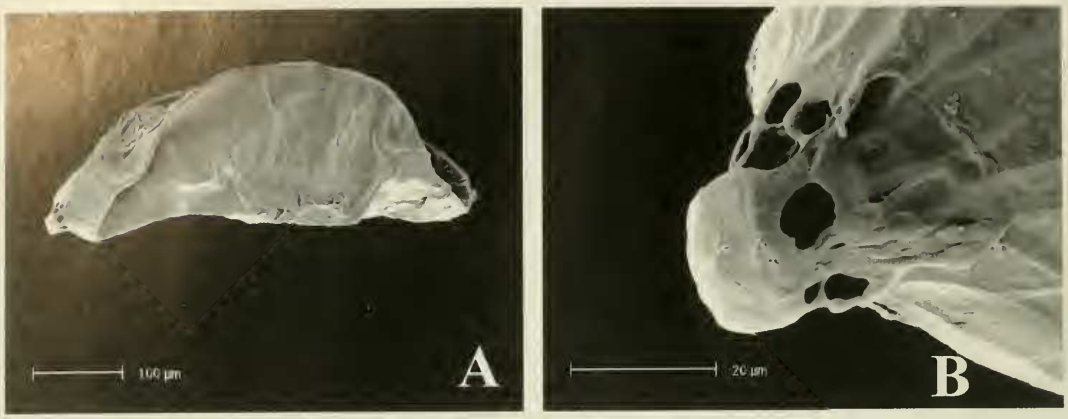

Fig. 2. Egg of *Tephritis footei:* (A) habitus, anterior to left; (B) pedicel showing pattern and shapes of aeropyles.

18.ix.1991; RDG/JAT, coll.; reared from flower heads of *S. canadensis* (1 ♀ to USNM). 4 ♂; Antelope Spring; Inyo National Forest., Inyo County; T17S, R35E, S24; 15.ix.1982; RDG, coll.; reared from flower head of *S. confinis* Nuttall (2 ♂ to USNM). 1 ♂; Kennedy Meadows, Sequoia National Forest; Inyo County; T22S, R35E, S24; 25.ix.1980; RDG, coll.; reared from flower head of *Euthamia* (formerly *Solidago*) *occidentalis* Nuttall (1 ♂ to USNM). 1 ♂; Round Valley Reservoir at 1,372 m; Plumas National Forest; Plumas County; 10.ix.1986; RDG, coll.; reared from flower head of *E. occidentalis* (1 ♂ to USNM).

Etymology.—*Tephritis headricki* is named for my friend, last Ph.D. student, and research collaborator, David H. Headrick, who as my successor in California tephritidology hopefully will one day study and publish the life history and describe the immature stages of his tephritid namesake.

Immature stages.—The egg, first-, second-, and third-instar larvae of *Tephritis footei* are described below.

Egg.: Five eggs measured *in situ* in field-collected, preblossom flower heads plus a total of five ova dissected from two females were white, opaque, smooth, elongate-ellipsoidal, 0.52 ± 0.007 (range, 0.48–0.56) mm long, 0.16 ± 0.005 (range, 0.14–0.18) mm wide, smoothly rounded at tapered basal end (Fig. 2A); pedicel button-like, 0.02 mm long, circumscribed apically by different-sized, semicircular aeropyles arranged singly or in rows of two parallel to the long axis of the egg (Fig. 2B).

The egg of *T. footei* (Fig. 2A), like those of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), differs from eggs of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993) by lacking prominent polygonal reticulation of the chorion. Also, the egg of *T. footei,* like those of *T. teerinki* and *T. joanae,* apparently is covered by a smooth, membraneous sheath (Figs. 2A, B; Goeden 2001b, c), which remains intact and is not partly shed and peeled back during oviposition as in the other two species. The function of this membraneous sheath remains unknown. It was first reported for *T. arizonaensis* by Goeden et al. (1993), who then belatedly recognized it in *T. baccharis,* and apparently it only has been reported to date from the eggs of these five species of *Tephritis.* In *T. arizonaensis* (Goeden et al. 1993), this membraneous sheath also is prominently, longitudinally striated. Weak longitudinal striations are present at the anterior, pedicellar end of the egg of *T. footei* (Figs. 2A, B), but otherwise are not seen on the rest of the egg body.

First instar larva: White, cylindrical (Fig. 3A); gnathocephalon conical; dorsal sensory organ well-defined, round, flattened (Fig. 3B-1); anterior sensory lobe (Fig. 3B-2) with ter-

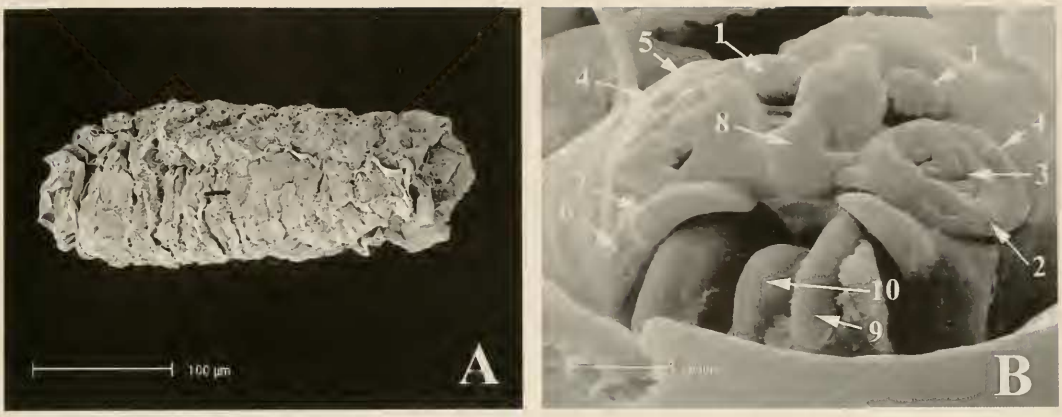

Fig. 3. First instar of *Tephritis footei:* (A) habitus, anterior to left; (B) gnathocephalon, ventrofrontal view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—stomal sense organ, 7—"lateral" integumental petal, 8—"median" integumental petal, 9—mouthhook, 10—median oral lobe.

minal sensory organ (Fig. 3B-3), lateral sensory organ (Fig. 3B-4), supralateral sensory organ (Fig. 3B-5), and pit sensory organ not seen; stomal sense organ (Fig. 3B-6) ventrolaterad of anterior sensory lobe and fused with flattened, protrudent, "lateral" integumental petal (Fig. 3B-7) dorsad of each mouthhook, one "median" integumental petal between anterior sensory lobes (Fig. 3B-8); mouthhook (Fig. 3B-9) bidentate (not shown); median oral lobe laterally compressed, apically rounded (Fig. 3B-10). Remaining characters could not be seen on the few specimens examined.

Only the first instar of *T. teerinki* has been described in detail (Goeden 2001c) for which this partial description for *T. footei* provides at least some basis for comparison. For example, it is worth noting that an integumental petal fused with the stomal sense organ (Figs. 3B-6, -7) also distinguished the first instar of *T. teerinki* (Goeden 2001c) and the first instars of at least five species of *Neaspilota* (Goeden 2001a) from subsequent instars. This character was first reported for the first instar of *Trupanea vicina* (Wulp) (Goeden and Teerink 1999).

Second instar larva: White, cylindrical, rounded anteriorly, truncated posteriorly, body segments well-defined (Fig. 4A); gnathocephalon not seen; anterior thoracic spiracle with five, subglobose or subquadrate papillae (Fig. 4B); lateral spiracular complexes not seen; posterior spiracular plate bears three ovoid rimae (Fig. 4C-1), ca. 0.02 mm long, and four interspiracular processes (Fig. 4C-2), each with one or two, lanceolate branches, each with one or two apical teeth, longest branch measuring 0.01 mm; stelex sensillum ventrolaterad (Figs. 4C-3, D-1) of posterior spiracular plate, dorsolateral stelex sensillum observed, but not shown; no other sensillum seen at lateral position; intermediate sensory complexes (Fig. 4D-2) with a stelex sensillum (Fig. 4D-3) and a medusoid sensillum (Fig. 4D-4).

The habitus of the second instar of *T. footei* (Fig. 4A) approximates those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c). Again, the partial description for *T. footei* allowed limited comparison with the second instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), the only species described in sufficient detail to date to allow full comparison of characters. The anterior spiracle of second instar *T. footei* bears five, subglobose or subquadrate papillae (Fig. 4B), like that of *T. joanae* (Goeden 2001b), not four, doliform papillae like *T. teerinki* (Goeden 2001c). Only minor differences in

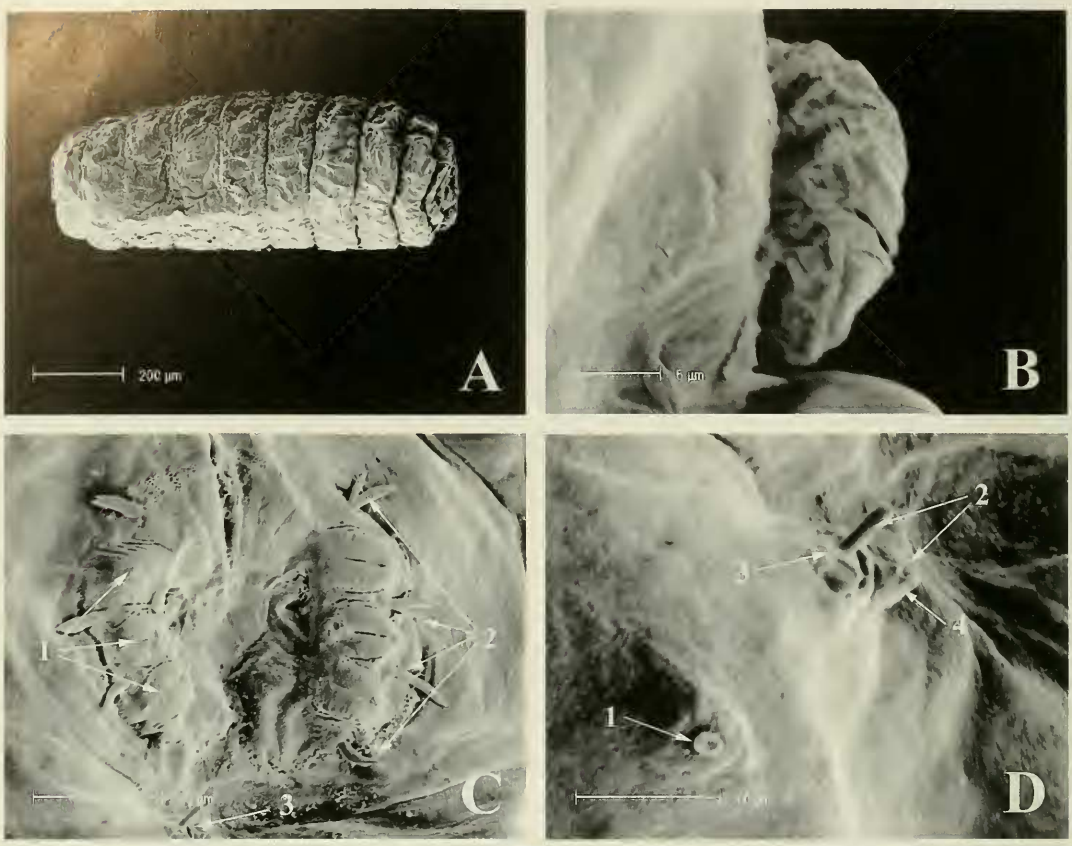

Fig. 4. Second instar of *Tephritis footei:* (A) habitus, anterior to right; (B) anterior spiracle; (C) caudal segment, 1—rimae, 2—interspiracular processes, 3—ventrolateral stelex sensillum; (D) 1—ventrolateral stelex sensillum, 2—intermediate sensory complex, with 3—stelex sensillum and 4—medusoid sensillum.

the number of branches on the interspiracular processes, i.e., one to two for *T. footei* (Fig. 4C-2), one to three for *T. teerinki* (Goeden 2001c), versus two to four for *T. joanae* (Goeden 2001b), were noted. Also, the branches of the interspiracular processes of *T. footei* are lanceolate (Fig. 4C-2), not foliose, like those of the second instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c).

Third instar larva: White, ellipsoidal, distinctly segmented, tapered anteriorly, truncated posteriorly (Fig. 5A); gnathocephalon conical, anteriorly flattened, and medially divided by a vertical suture (Fig. 5B-1); posteriorly directed, spinose, minute acanthae incompletely circumscribe prothorax anteriorly (Figs. 5B-2, C-12), instead many round to elongate-rounded, integumental petals circumscribe central half of prothorax (Fig. 5B-3); dorsal sensory organ well-defined, hemispherical (Fig. 5C-1); anterior sensory lobe (Fig. 5C-2) bears terminal sensory organ (Fig. 5C-3), lateral sensory organ (Fig. 5C-4), supralateral sensory organ (Fig. 5C-5), and pit sensory organ (Fig. 5C-6); two medial, papilliform integumental petals (Fig. 5C-7) and two, lateral, spatulate, integumental petals (Fig. 5C-8) in two rows above each mouthhook (Fig. 5C-9), lower lateral petal continuing laterally around oral cavity, and separate from stomal sense organ (Fig. 5C-10) ventrolaterad of anterior sensory lobe; at least three complete oral ridges (Fig. 5C-11) laterad of each anterior sensory lobe; mouthhook apparently bidentate; median oral lobe

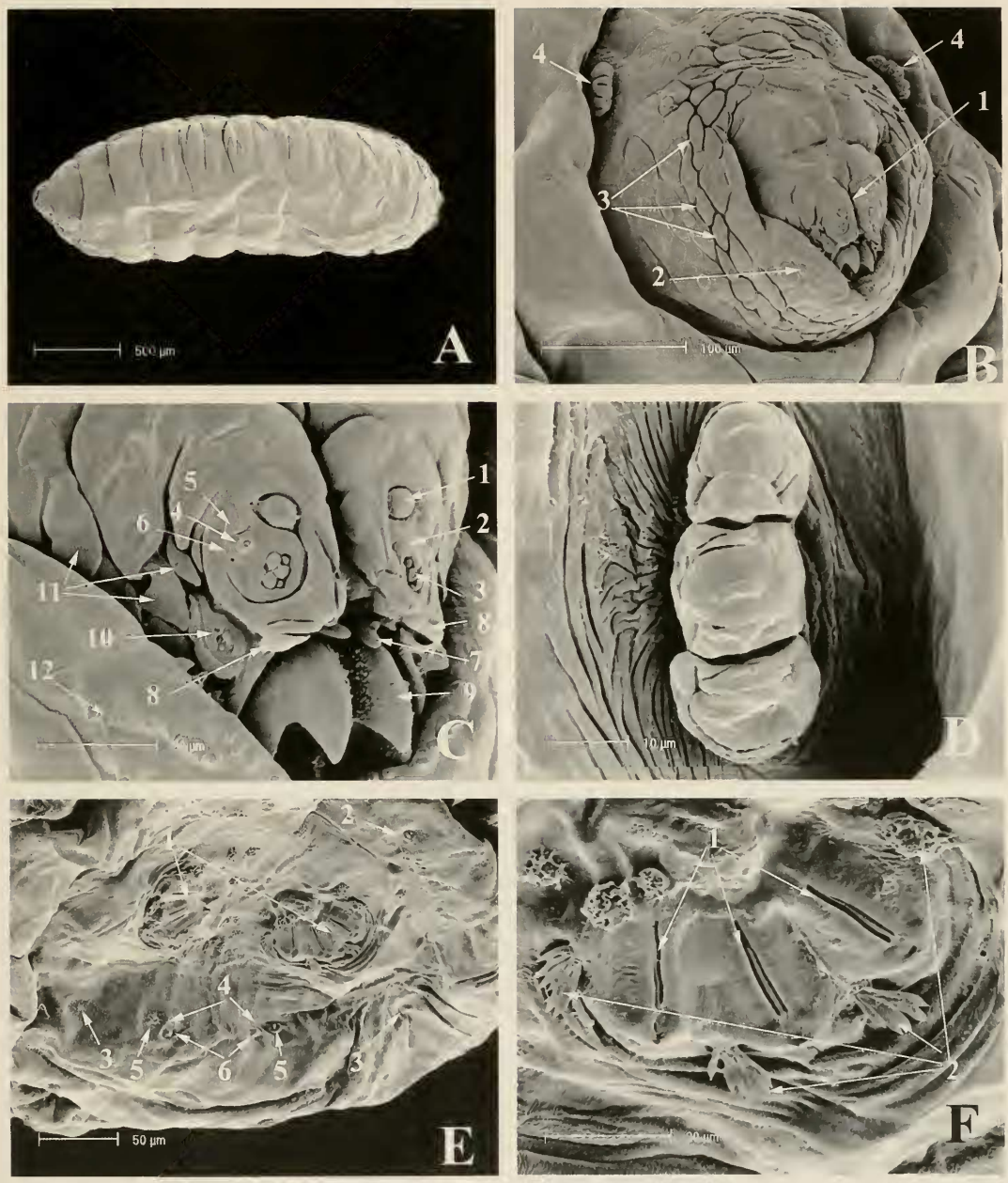

Fig. 5. Third instar of *Tephritis footei:* (A) habitus, anterior to left; (B) gnathocephalon and prothorax, frontolateral view, 1—vertical medial suture of gnathocephalon, 2—minute acanthae, 3—integumental petals on prothorax, 4—anterior spiracle; (C) gnathocephalon, frontolateral view, 1—dorsal sensory organ, 2—anterior sensory lobe, 3—terminal sensory organ, 4—lateral sensory organ, 5—supralateral sensory organ, 6—pit sensory organ, 7—medial integumental petal, 8—lateral integumental petal, 9—mouthhook, 10—stomal sense organ, 11—oral ridges, 12—minute acanthae; (D) anterior spiracle; (E) caudal segment, 1—spiracular plates, 2—dorsolateral stelex sensillum, 3—ventrolateral stelex sensillum; 4—intermediate sensory complex, with 5—stelex sensilla and 6—medusoid sensillum; (F) posterior spiracular plate, 1—rimae, 2—interspiracular processes.

present, but only partially seen and not pictured; anterior thoracic spiracle on posterior margin of prothorax bears three (not shown) or four subglobose or subquadrate papillae (Figs. 5B-4, 5D); mesothoracic, metathoracic, and abdominal lateral spiracular complexes not seen; each posterior spiracular plate (Fig. 5E-1) surrounded by a pair of dorsolateral stelex sensilla (Fig. 5E-2) and ventrolateral pair of stelex sensilla (Fig. 5E-3); each posterior spiracular plate bears three ovoid rimae (Fig. 5F-1), ca. 0.02 mm in length, and four, three- to four-branched, single-, bi- or trifurcately-tipped, interspiracular processes, each ca. 0.05 mm long (Fig. 5F-2); intermediate sensory complex (Fig. 5E-4) with a stelex sensillum (Fig. 5E-5) and a medusoid sensillum (Fig. 5E-6).

The habitus of the third instar of *T. footei* differs from those of four other described congeners in at least two ways. The elongate-ellipsoidal shape of the third instar of *T. footei* (Fig. 5A) appears intermediate to the ovoidal shape of the third instars of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c) and the cylindrical shape ascribed to third instars of *T. baccharis* (Goeden and Headrick 1991) and *T. arizonaensis* (Goeden et al. 1993). The prothorax (Fig. 5B-1) is circumscribed by many more integumental petals than the much smoother prothoracic segments of the four other species of *Tephritis* examined to date (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c). Fewer minute acanthae anteriorly circumscribe the prothorax of the third instar of *T. footei* (Fig. 5B-2) than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c). On the other hand the gnathocephalon, or at least the anterior sensory lobes of all five species are separated by a vertical medial suture (Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c; Fig. 5B).

The integumental petals in the third instars of all five congeners examined to date are arranged in a double row above each mouthhook, but those of *T. footei* (Fig. 5C-8) occur in two rows of two like *T. teerinki* (Goeden 2001c), with an additional, medial pair of different shape in *T. footei* (Fig. 5C-7). However, the integumental petals of both *T. teerinki* (Goeden 2001c) and *T. footei* (Figs. 5C-7, 8) are fewer in number than those of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b). Both *T. footei* and *T. teerinki* also apparently lack the additional integumental petals found in a vertical double row above these papillae, one pair to each side of the medial depression separating the anterior sensory lobes (Fig. 5C-2; Goeden and Headrick 1991; Goeden et al. 1993; Goeden 2001b, c). The integumental petals increase in number between the last two instars of *T. footei* (Figs. 5C-7, 8), *T. joanae* (Goeden 2001b), and *T. teerinki* (Goeden 2001c).

The mouthhooks of the third instars of *T. footei* (Fig. 5C-9), like those of *T. teerinki* (Goeden 2001c), appear bidentate, unlike the tridentate mouthhooks of *T. baccharis* (Goeden and Headrick 1991), *T. arizonaensis* (Goeden et al. 1993), and *T. joanae* (Goeden 2001b). However, most of the nine specimens of third instar *T. footei* examined by SEM had their mouthparts hidden, which precluded examination of the oral cavity and mouthhooks in ventral view.

The anterior spiracle of the third instar of *T. footei* (Fig. 5D) bore three or four papillae, one or two less than the second instar, but not three in the second instar and three or four in the third instar, like *T. joanae* (Goeden 2001b), or four in the second instar and five in the third instar as reported for *T. teerinki* (Goeden 2001c).

Goeden (2001c) discussed the stelex sensilla surrounding the posterior spiracular plates of the third instars that apparently differ in number among the *Tephritis* species examined to date. However, the caudal segment of the third instar of *T. footei*, like those of *T. joanae* (Goeden 2001b) and *T. teerinki* (Goeden 2001c), apparently are surrounded by a dorsolateral and ventrolateral pair of stelex sensilla (Figs. 5E-2, 3) as well as a ventral pair of intermediate spiracular complexes

(Fig. 5E-4), the medusoid sensilla of each bears short apical papillae typical of this type of chemosensillum (Goeden 2001a, b, c; Goeden and Teerink 1999, and references therein).

Puparia: All puparia prepared for SEM unfortunately turned out to be *Campiglossa clathrata* (Loew), which imperfectly, temporally partitions and thus shares the flower heads of *A. tridentata* with *T. footei*, i.e., symphagy (Goeden 1997). Other puparia examined, identified, and measured *in situ* provided the basis for the following abbreviated description.

Dull black, ellipsoidal, and smoothly rounded at both ends. Thirty-four puparia averaged 1.87 ± 0.02 (range, 1.63–2.13) mm in length; 0.98 ± 0.013 (range, 0.85–1.14) mm in width.

Distribution and Hosts

To date, *Tephritis footei* is only known from California and from flower heads of *Artemisia tridentata*; however, it has been reported elsewhere by me (Goeden 1993), and probably by others, as *T. ovatipennis*, and this should be corrected. Accordingly, *T. footei*, possibly may be a nearly monophagous, widely distributed species on *A. tridentata*, which itself is widely distributed throughout the western United States (Hickman 1993), and belongs to the subtribe Artemisiinae of the Tribe Anthemideae (Bremer 1994). This monophagy is presumed because *T. araneosa*, as now constituted, has been reared from flower heads of four other California species of *Artemisia*, i.e., *A. californica* Lessing, *A. douglasiana* Besser, *A. dracunculus* L., and *A. ludoviciana* Nuttall, the last-named plant formerly was reported as a host of *T. ovatipennis* by Goeden (1993), which now should be deleted; whereas, *A. dracunculus* is a new host record for *T. araneosa* (Goeden 1993). As noted above, *T. araneosa*, or what is probably a separate new species near *araneosa*, also has been reared by me from *Chrysothamnus nauseosus* (Pallas) Britton, *C. parryi* (A. Gray) E. Greene, *C. teretifolius* (Durand and Hilgard) H. M. Hall, *C. viscidiflorus* (Hooker) Nuttall, and *Ericameria* (as *Haplopappus*) *bloomeri* (A. Gray) J. F. Mcbride, most of which were reported as hosts of *T. araneosa* by Goeden (1993), except for this newly confirmed host record for *C. nauseosus* in Wasbauer (1972). *Chrysothamnus* and *Ericameria* both belong to the subtribe Solidagininae of the tribe Astereae (Bremer 1994). Also as noted above, *T. headricki* is an oligophagous tephritid, reared solely from the flower heads of two species of *Solidago*, i.e., *S. canadensis* and *S. confinis* and *Euthamia occidentalis*, all three of which belong to the subtribe Solidagininae of the tribe Astereae (Bremer 1994). The first two plant species were reported as hosts of *T. ovatipennis* by Goeden (1993), which now need to be deleted, and the latter plant represents a new host-plant genus and species record for *Tephritis*. *Tephritis headricki* undoubtedly has additional hosts as yet undiscovered, and probably is a widespread species like its widespread and diverse host-plant genus, *Solidago* (Hickman 1993). Goeden (2001c) also removed *Hulsea* spp. from those hosts reported by Goeden (1993) as *T. ovatipennis*, when he described *T. teerinki*. The three specimens identified and reported by Goeden (1993) for *T. ovatipennis* reared from *Machaeranthera canescens* (Pursh) A. Gray, upon re-examination were re-identified and confirmed with other reared specimens as *T. michiganesis* Quisenberry; this finding extends its distribution across the western United States to southern California from western Minnesota/eastern North Dakota, and represents the first host-plant record for this tephritid (Foote et al. 1993). Therefore, as presently constituted, *T. ovatipennis* represents an oligophagous species reared from two species of *Erigeron*, i.e., *E. foliosus* Nuttall and *E. glaucus* Ker-Gawler, and *Trimorpha lonchophyllus* (Hooker) G. Nesom, all of which belong to the subtribe Asterinae of the tribe Astereae. Of the last three species, the first named is a new host-plant record; the second and third species were reported as hosts of *T. ovatipennis* by Goeden (1993), the third also as another species of *Erigeron* (Hickman,

1993). Recent revisions by plant and insect taxonomists (Hickman 1993; Bremer 1994; Goeden 2001a, b) have helped to clarify and better interpret the host affinities of these California *Tephritis* since Goeden (1993), but continued study is needed of these and other *Tephritis* belonging or not to the "*araneosa* complex."

Biology

Egg.—In each of 11, closed, preblossom, immature flower heads of *Artemisia tridentata* a single egg of *T. footei* was inserted pedicel-last through one or more phyllaries into an ovule (Fig. 6A). Thus, the 11 eggs each rested with their long axes at a 45° to 60° angle to the receptacles of the young flower heads and an average of one ovule/floret was damaged per flower head by oviposition. Thus, about 25% of an average total of 4.3 ± 0.2 (range, 3–7) ovules/florets counted in 27 infested, closed preblossom flower heads were damaged by oviposition. The receptacles of preblossom heads that contained eggs averaged 0.36 ± 0.02 (range, 0.28–0.4) mm in diameter.

Larva.—Upon eclosion, the single first instars found feeding in seven, closed, preblossom flower heads tunneled immediately into a floret and then continued to feed parallel to the receptacle on one or more ovules (Fig. 6B). The receptacles of these seven infested flower heads averaged 0.39 ± 0.02 (range, 0.28–0.46) mm in diameter and an average of 1.8 ± 0.49 (range, 1–3) ovules was damaged in these seven flower heads. No receptacle was abraded or pitted by larval feeding. Thus, about 42% (range, 25–70%) of an average total of 4.3 ovules/florets counted for the above-mentioned, 27 flower heads were damaged by the first instars.

Second instars (Fig. 6C) continued feeding on ovules in closed, preblossom flower heads. They fed with their bodies perpendicular to the receptacles, but always well above the receptacles (Fig. 6C). Receptacles of 25 flower heads containing second instars averaged 4.30 ± 0.22 (range, 2.28–6.84) mm in diameter. These eight flower heads each contained a single larva that had damaged a single ovule, or again, about 25% of the average total of 4.3 ovules/florets per flower head counted within the above-mentioned, 27 flower heads.

Third instars in flower heads fed with their long axes oriented perpendicular to the receptacles, and with their mouthparts commonly directed towards (Fig. 6D), or less commonly, away from the receptacles (Fig. 6E). All of the ovules/florets in each of the heads were destroyed (Figs. 6D, E). The receptacles were abraded or pitted in two (64%) of nine, closed flower heads containing third instars, or the larvae were found feeding on the basal fragments of the ovules connected to the receptacles, which suggested that sap constituted at least part of the diet of third instars of *T. footei*, probably towards the end of the third stadium. Goeden (1988b), Headrick and Goeden (1990), Goeden and Headrick (1992), Goeden et al. (1993, 1995), Headrick et al. (1996), Goeden and Teerink (1997) first noted, described, and discussed sap feeding by florivorous species of Tephritidae in the genera *Trupanea, Paracantha, Neaspilota, Tephritis, Urophora, Dioxyna,* and *Xenochaeta,* respectively. Upon completing feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and formed puparia (Fig. 6F).

Pupa.—The receptacles of 43 flower heads, each of which contained a single puparium (Fig. 6F) averaged 0.6 ± 0.04 (range, 0.42–1.42) mm in diameter. The receptacles were abraded or pitted in 19 of 43 (44%) flower heads containing puparia, further confirming that sap constituted part of the diet of the third instars. All of the contents of these flower heads were destroyed and the puparia occupied most of the flower heads (Fig. 6F).

Adult.—Adults (Fig. 6G, H) apparently are long-lived and constitute the only overwintering stage in southern California. Under insectary conditions, six unmated females (Fig. 6G) lived an average of 87 ± 8 (range, 71–120) days, and five virgin males (Fig. 6H) averaged 64 ± 12 (range, 18–91) days. Such

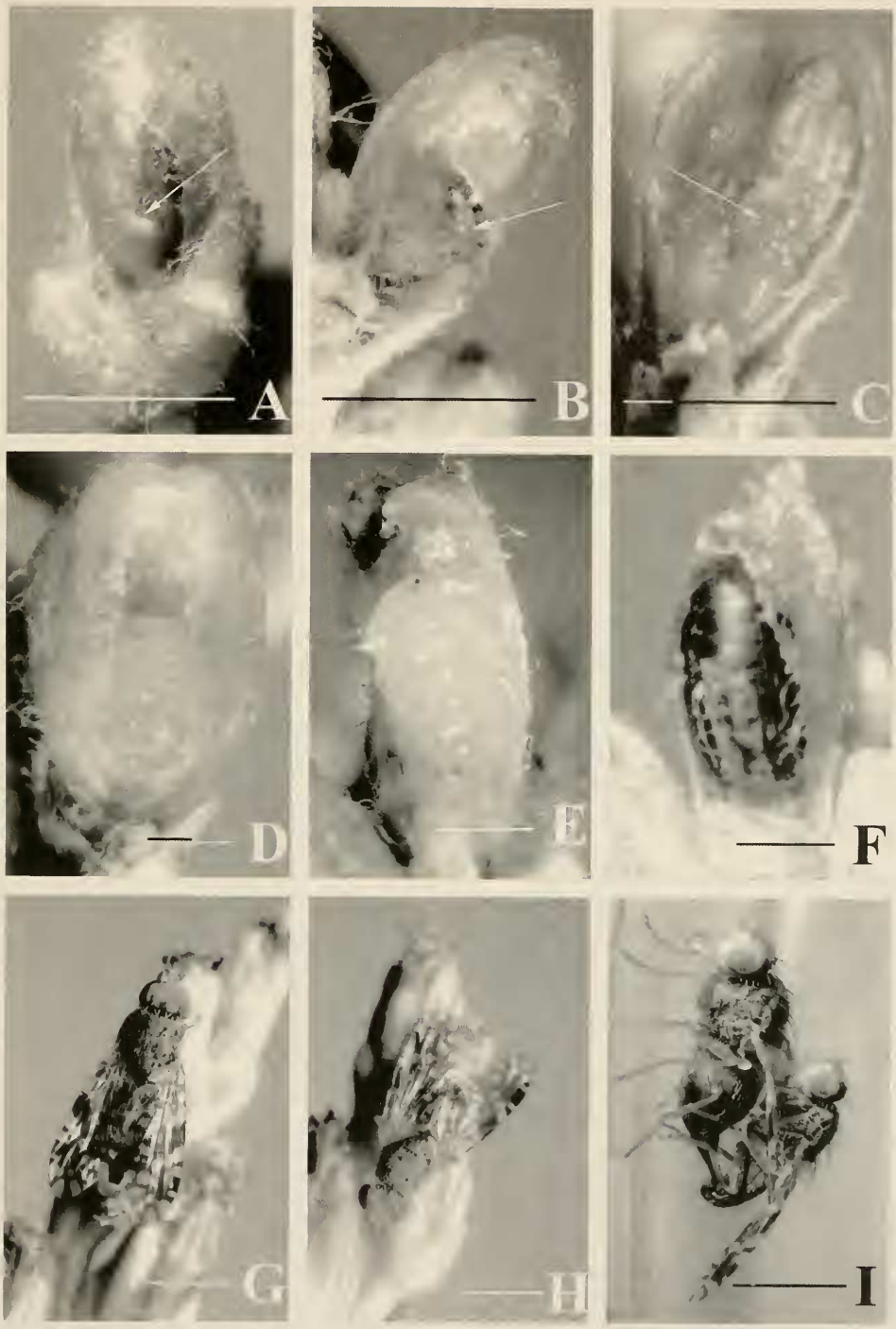

Fig. 6. Life stages of *Tephritis footei* in flower heads of *Artemisia tridentata:* (A) egg (arrow) in closed, preblossom flower head inserted into floret; (B) first instar (arrow) feeding within floret in preblossom flower head; (C) second instar (arrow) feeding in adjacent florets in preblossom flower head; (D) third instar feeding on receptacle in closed, preblossom flower head; (E) full-size, third instar positioned for pupariation; (F) single puparium occupying interior of flower head; (G) adult female; (H) adult male; (I) mating pair with female forming droplet. Lines = 1 mm.

lengthy longevities are commensurate with the aggregative type of life history possessed by this tephritid (Headrick and Goeden 1994, 1998).

The premating and mating behaviors of *T. footei* were not studied in the field, but were limitedly observed in petri dish arenas of the type otherwise found to be so useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors occasionally observed with *T. footei* were tracking and side-stepping by males (Headrick and Goeden 1994). The most common wing display was asynchronous supination by both sexes, both spontaneous and in response to other individuals (Goeden et al. 1993; Headrick and Goeden 1994, 1999). Males did not exhibit any of the common tephritid courtship displays, including regular, abdominal pleural distension. Four pairs were observed to mate (Fig. 6I) once or twice per day for a total of 10 matings that lasted an average of 208 (range, 84–316) min. Copulatory induction behavior (CIB) (Headrick and Goeden 1994, 1999), and the copulatory positions attained by each sex, generally were as described for *T. arizonaensis* (Goeden et al. 1993). Separation of a male and female was observed three times, with the male turning and rapidly walking off and away from the female while pulling free his genitalia.

Seasonal history.—The life cycle of *T. footei* on *Artemisia tridentata* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the adult is the principal overwintering stage. Consequently, come late-spring/early summer (May to June), adults aggregate on preblossom shoots and subsequently oviposit in the small, newly-formed, closed, preblossom flower heads. The larvae feed until fully grown, then pupariate in flower heads and emerge in midsummer (late-June to July). They spend the rest of the summer and fall, probably as non-reproductive adults, feeding in mountain meadows and riparian habits where they subsequently overwinter. Or, possibly two overlapping, nondescrete generations are produced starting earlier on lower-elevation, or later on higher-elevation, host plants.

Natural enemies.—*Halticoptera* sp. and *Mesopolobus* sp. (Hymenoptera: Pteromalidae) were reared from separate puparia of *T. footei* as solitary, larval-pupal endoparasitoids. Many additional specimens of both species were reared from caged mature flower heads of *A. tridentata* as probable parasitoids.

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